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OBSERVATIONS ON THE SPECIES OF RHOPALOCERA COMMON TO MADAGASCAR AND THE ORIENTAL REGION.

By the late A. Steven Corbet, D.Sc., Ph.D., F.R.I.C., F.R.E.S.
(*British Museum, Natural History.*)

Manuscript received 11th February, 1948.

(Read 1st September, 1948.)

With 13 Text-figures.

A special interest attaches to the fauna of Madagascar, as many of its animal groups show an affinity with Oriental rather than with Aethiopian forms, and it is supposed that, in some cases, this relationship is attributable to a former land connection between Madagascar and Indo-Malaya. It is believed that, in Mesozoic times, a large land area (now termed *Gondwanaland*, but referred to as *Lemuria* by Sclater), stretched across the Indian Ocean from Africa to India, and perhaps even to Australia, and that for some time Madagascar formed a part of this continent. It seems certain that nothing in the way of an effective land bridge between East Africa and the Indian Region remained as late as the early Tertiary, and, although united with the African mainland during the earlier part of this era, it appears that Madagascar was finally separated from the continent during the Miocene.

Flowering plants first appeared in the Cretaceous, but the earliest known fossil butterflies cannot, with any certainty, be dated earlier than the Eocene. So any Oriental affinities present among the Madagascan butterflies cannot be attributed to any former land connection across the Indian Ocean.

The total number of butterfly species in Madagascar is not known with much precision, probably it lies between 250 and 300 (Mabille, 1885, 1887), and at least 90 per cent. of the total comprises species which are otherwise strictly Aethiopian in distribution. Leaving aside these purely African species, there are present in Madagascar two groups of butterflies which are of interest in the present discussion :

(A) Those representing *genera* (or groups of genera) which are present also in the Oriental Region, but absent from, or sparsely represented on, the African mainland.

(B) *Species* common to Madagascar and the Oriental Region. Most, but not all, of these occur also on the African mainland, and a few of them have even reached America.

(A) Genera and Groups of Genera common to Madagascar and the Oriental Region, but absent from, or sparsely represented on the African Mainland.

I have found only four genera (or groups of genera) of butterflies confined, or almost confined, to Madagascar as far as the Aethiopian Region is concerned, but which appear to be definitely Oriental in origin.

Genus **Atrophaneura** Reakirt (Papilionidae).

Although this genus is strongly represented in the Oriental Region and in America, the only Aethiopian species is *A. antenor* (Drury), which is confined to Madagascar. While the facies of this butterfly suggests a species of *Atrophaneura*, closer examination does not entirely support this classification, for the male genitalia are characteristic of *Papilio* Linnaeus (fig. 1), and the well-defined anal fold on the hind wing, which encloses a scent organ, and is present in most species of *Atrophaneura*, is lacking. On the other hand, the larva and pupa of *A. antenor* resemble those of *Atrophaneura* and the other Aristolochia swallow-tails, although, in this case, the larval food plant is *Quisqualis grandidieri* Baill. (Combretaceae) and not one of the Madagascan species of Aristolochiaceae.

Genus **Henotesia** Butler (Satyridae).

The *Mycalesis* group of genera is distributed throughout the Indo-Australian and Aethiopian Regions, and comprises a few genera which can be sharply differentiated. On the fore wing the lower discocellular vein is proximally curved in *Mycalesis* Hübner (with over 80 species in the Indo-Australian Region), while it is straight and sharply angled in the middle in *Henotesia* Butler (30 species in Madagascar and 13 species on the African mainland); in this respect the genus *Monotrichtis* Hampson (about 60 species on the African mainland) is rather intermediate (fig. 2). The eyes are naked in *Monotrichtis*, but smooth in *Mycalesis* and *Henotesia*.

Several of the *Monotrichtis* species have facies very similar to those found in certain of the *Mycalesis* species, while the *Henotesia* forms are more distinct, although *Henotesia narcissus* (Fabricius), from Madagascar and the Comoro Islands, and *Mycalesis anapita* Moore, from Malaysia, are remarkably similar in appearance (fig. 3).

Genus **Smerina** Hewitson (Nymphalidae).

This monotypical genus is confined to Madagascar and differs from the allied Oriental genera *Cirrochroa* Doubleday and *Vindula* Hemming in that the eyes are hairy. In general appearance *S. manoro* Ward most closely resembles a species of *Cirrochroa*, but nothing is known regarding the early stages of the insect.

Genera **Arnetta** Watson and **Fulda** Evans (Hesperiidae).

The genus *Arnetta* is represented by four species in the Oriental Region and three in Madagascar, and it is not found on the African mainland. All four species in the closely allied genus *Fulda* are confined to Madagascar. Nothing is known regarding the life-history of any species in the group.

There are seven or eight genera of Rhopalocera (mostly Hesperiidae) confined to Madagascar, but none of them has close affinities with any Oriental genus.

(b) Species of Rhopalocera common to Madagascar and the Oriental Region.

The species of butterflies common to Madagascar and the Oriental Region can be divided into the following groups (*a*) to (*d*) according to their distributions elsewhere. All frequent secondary growth, and all are found on the plains in

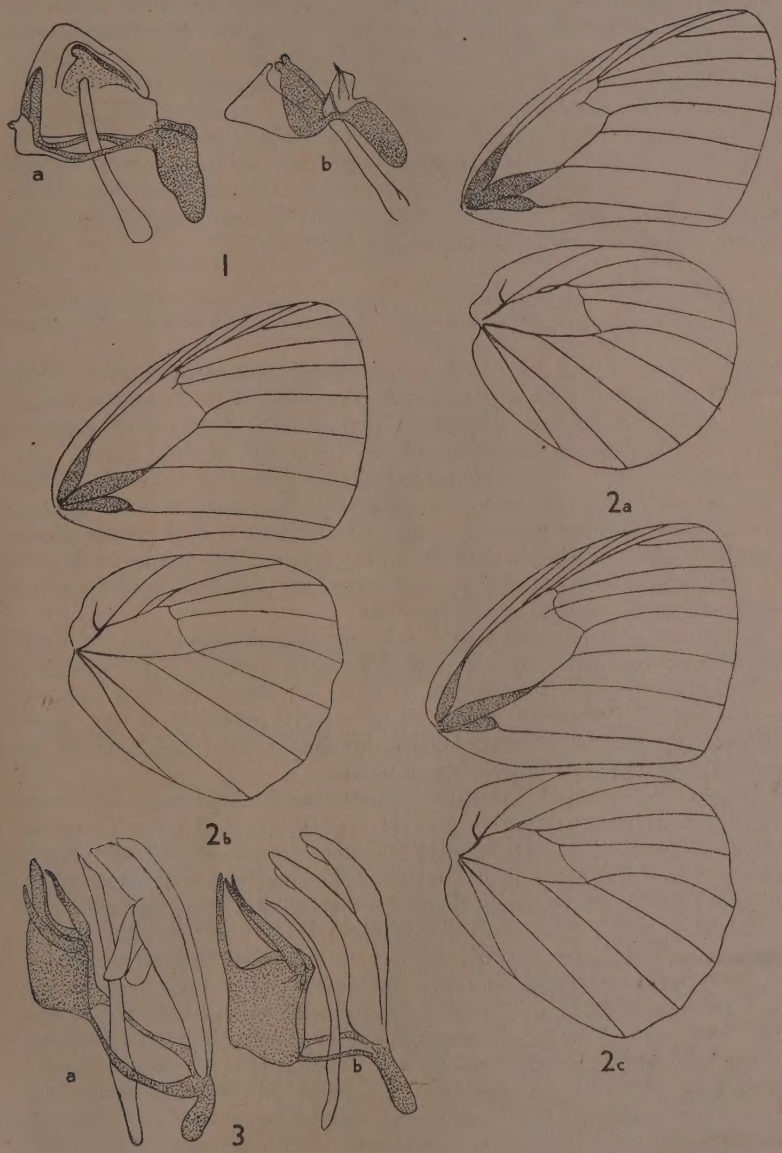

FIG. 1.—Male genitalia (lateral view) of (*a*) *Atrophaneura antenor* (Drury), Madagascar, and (*b*) *A. aristolochiae* (Fabricius), India. Right valva removed in both figures.

FIG. 2.—Wing venation of (*a*) *Henotesia narcissus* (Fabricius), ♂, Madagascar ; (*b*) *Mycalesis anapita* Moore, ♂, Malaya, and (*c*) *Monotrichtis safitza* (Hewitson), ♂, East Africa.

FIG. 3.—Male genitalia (lateral view) of (*a*) *Henotesia narcissus* (Fabricius), Madagascar, and (*b*) *Mycalesis anapita* Moore, Malaya.

Ceylon and Malaysia, except *Eurema brigitta* and *Vanessa cardui*, which are confined to the hills in Malaysia, and *Anaphaeis aurota* and *Precis lintingensis*, which are non-Malaysian. So many of the species present unusual features, that they are considered individually. It may be understood that there are no differences between the male genitalia of the corresponding Malagasy and Oriental forms, unless such is explicitly stated to be the case.

In addition to the species mentioned, there are one or two other species or species-complexes found in tropical Africa and Indo-Malaya, but absent from Madagascar. Most interesting of these is the Oriental *Argynnis hyperbius* (Linnaeus), which is found in Africa only in Abyssinia.

(*a*) Circumtropical species present in Madagascar (*Precis orithya* (Linnaeus), *Vanessa cardui* (Linnaeus), *Hypolimnas misippus* (Linnaeus) and *Zizula hylax* (Fabricius)).

Precis orithya (Linnaeus). It has been shown elsewhere (Corbet, 1948) that the American *P. lavinia* (Cramer) is conspecific with *P. orithya*, which latter butterfly is distributed throughout tropical Africa, and, in the Oriental Region, extends from Arabia eastwards to India and Ceylon, Japan, New Guinea and Australia. The male genitalia of *P. orithya* and *P. lavinia* show no more than subspecific differences, although the American forms are strongly differentiated in facies, the sexes being quite similar, and the male almost lacking the bright blue coloration of the upper surface. The species is divisible into a number of distinct subspecies, indicating long periods of isolation of the races without reinforcement by immigration.

Vanessa cardui (Linnaeus) is so widely distributed throughout the world that its absence from an island of the size of Madagascar would be more remarkable than its presence. Nevertheless, it is by no means common in many tropical countries, where it appears to be mainly restricted to the higher elevations. A single form occurs almost throughout the whole range of the species. The larva feeds on a variety of plants.

Hypolimnas misippus (Linnaeus) is remarkable for its strong sex dimorphism, the female being an almost exact replica of *Danaus chrysippus* (Linnaeus), which latter species, however, is not found in America. In the Old World, *H. misippus* is found throughout tropical Africa and passes through Arabia to India and Ceylon, and extends eastwards through the Malay Archipelago to New Guinea and the Bismarck Archipelago. It is possible that, like its congenor *H. bolina* (Linnaeus), *H. misippus* has strong migratory tendencies, for it shows no geographical variation throughout its extensive range. Regarding the presence of *H. misippus* on Christmas Island (south-west of Java), Butler (1900) said: "The single example obtained is much rubbed and shattered; it was the only specimen seen, and appeared immediately after north-westerly gales, so there can be little doubt that it was blown over from Java."

H. misippus appears to be a comparatively recent introduction into America, and it is generally believed that it travelled from Africa in the old slave ships some four centuries or so ago, although on a few occasions it has been seen at sea in the Atlantic Ocean. At present it is found in the southern United States, some of the West Indian Islands, and in the northern parts of South America, but, usually, in isolated localities. It is possible *H. misippus* had its origin in Africa, where it is more abundant than in the East.

Zizula hylax (Fabricius) (= *gaika* (Trimen)) is one of the smallest butterflies, and is circumtropical in distribution. It occurs in tropical Africa, from Arabia to India and Ceylon, and eastwards to Australia, the Solomon Islands and New Hebrides, although apparently absent from New Guinea. In America it is found in Mexico and in the northern half of South America, where it is known as *Z. tulliola* (Godman and Salvin). The American representative has male genitalia identical with those found in the Old World form (as was pointed out by Stempffer (1934)), and, usually, but not invariably, the American form has a mid-cell spot on the fore wing beneath. Only slight geographical variation is shown by the species throughout its extensive range. *Z. hylax* is found on many of the more remote oceanic islands in the tropical belt.

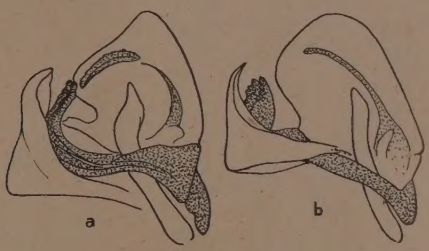

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Fig. 4.—Male genitalia (lateral view) of (*a*) *Papilio demoleus* (Linnaeus), Malaya, and (*b*) *P. demodocus* Esper, St. Principe. Right valva removed in both figures.

(*b*) Oriental species present in Madagascar, tropical Africa and Arabia (the *Papilio demoleus*-complex, *Anaphaeis aurota* (Fabricius), *Catopsilia pyranthe* (Linnaeus), *Eurema hecabe* (Linnaeus), *Danaus chrysippus* (Linnaeus), *Precis lintingensis* (Osbeck), *Zizeeria knysna* (Trimen), *Lampides boeticus* (Linnaeus) and *Pelopidas mathias* (Fabricius).

The *Papilio demoleus*-complex is represented almost throughout the warmer parts of the Old World by one or other of two "species" or forms which nowhere fly together, but meet in Arabia (fig. 5). In general appearance, these two are similar, although there are several constant differences, but the larvae appear to be indistinguishable. Although there is little more than a generic resemblance in the pattern of the male genitalia (fig. 4), it is evident that the Oriental *P. demoleus* (Linnaeus) and African *P. demodocus* Esper replace one another throughout their extensive range.

P. demoleus flies from North-east Arabia to India and Ceylon, China, New Guinea and Northern Australia; there is a surprising hiatus in the distribution, however, for the butterfly is absent from the Large Sunda Islands (Sumatra, Borneo and Java) the Philippines, Celebes and Moluccas, although a common insect in the Malay Peninsula. Where it occurs, *P. demoleus* is common in gardens and cultivated districts, as the larva feeds on citrus, as well as on certain wild species of Rutaceae. Wiltshire (1945) considered that the eastern *P. demoleus* probably reached Arabia from India *via* South Persia and Muscat, by importation by man of the larval food plant citrus in historical times.

The Aethiopian *P. demodocus* occurs in South-west Arabia, tropical Africa and Madagascar. On the last-named island are three further species belonging to the *P. demoleus*-complex, one of which *P. erithioides* Grose Smith, more closely resembles *P. demoleus* than does *P. demodocus*.

The boundary in Arabia between the two major forms of *P. demoleus* is identical with that found between the two genitalia forms of *Zizeeria knysna* (fig. 5).

Anaphaeis aurota (Fabricius) (= *mesentina* (Cramer)). A widely distributed butterfly, ranging from Ceylon and India to Arabia, Palestine, Egypt and most

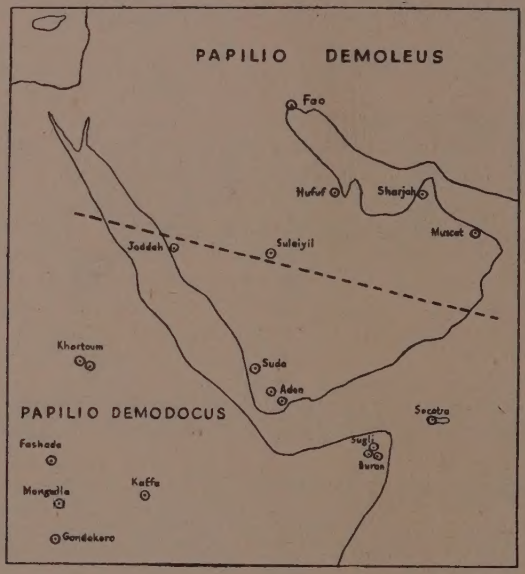

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FIG. 5.—*Papilio demoleus* Linnaeus and *P. demodocus* Esper in Arabia.

of Africa. It displays seasonal dimorphism and but little geographical variation, the nominotypical race flying throughout most of the range in Asia and Africa, although the Madagascan subspecies is quite distinct.

Catopsilia pyranthe (Linnaeus) is widely distributed throughout the Oriental Region, from Arabia to India and Ceylon, the Philippines, Australia and the Fiji Islands, but it appears to be absent from the Celebes, Moluccas and New Guinea. In those parts of Ceylon and India with alternating wet and dry seasons, a dry-season form known as *C. florella* (Fabricius) occurs, and has hitherto been regarded as a distinct species. Indeed, in Africa and Madagascar the butterfly is known by this latter name. Throughout the range of the species there is little subspecific variation.

Eurema hecabe (Linnaeus) is probably the commonest butterfly of the warmer regions of the Old World. Although feeble in flight, its range is

enormous: it shows marked individual variation, and it occurs in a large number of rather well-defined geographical races. In some parts of its range it gives rise to both wet- and dry-season forms. *E. hecabe* is distributed in tropical Africa and Madagascar, from Arabia to India and Ceylon, China and Japan, and eastwards through the Archipelago to Australia and the Fiji and Tonga Islands.

Danaus chrysippus (Linnaeus). This widely distributed species occurs in the eastern part of the Mediterranean Basin, almost throughout Africa, in Madagascar, and from Arabia eastwards to Australia, New Guinea and the New Hebrides. Throughout its range, the butterfly occurs in two or three well-defined polymorphic forms, but only seven geographical races have been recognized.

Precis lintingensis (Osbeck) (=*hierta* (Fabricius)) is distributed in tropical Africa, and through Arabia, Ceylon and India eastwards to China, but is not found south of Peninsular Siam. Curiously enough, this species has the same

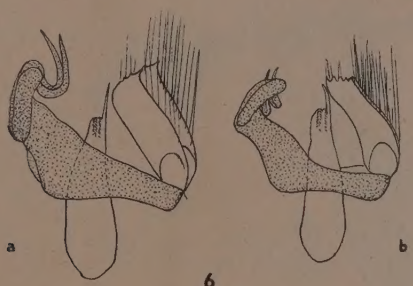

FIG. 6.—Male genitalia (lateral view) of (*a*) *Zizeeria knysna* (Trimen) form "*knysna*" Madagascar, and (*b*) *Z. knysna* (Trimen) form "*karsandra*," Burma.

type of male genitalia as *P. orithya*, and these two *Precis* species fly together almost throughout the range of *P. lintingensis*.

Zizeeria knysna (Trimen) (=*lysimon* (Hübner)). Formerly known under the preoccupied name of *Z. lysimon* (Hübner), this small, low-flying Lycaenid butterfly occurs on the Mediterranean coasts (including the Iberian Peninsula), almost throughout Africa, and in the greater part of the Indo-Australian Region. In the equatorial countries it seems to prefer the drier zones, and, except in Ceylon and India, it is rather rare. There is a tendency towards seasonal dimorphism, the male having narrower black borders on the upperside in the dry-season form. There is no marked division into subspecies, although, in some localities such as the Canary Islands (where the females are remarkably blue), the local representatives are sufficiently distinct to warrant denomination.

Two distinct types of male genitalia can be recognized, the oriental "*karsandra*" type, with the valva serrate, and the African "*knysna*" type, with the valva pointed, and this difference cannot be strictly correlated with a difference in facies (see Chapman, 1910) (fig. 6). In general, the underside of the fore wing has the post-discal spots blacker, more prominent and more broadly bordered with white in the "*karsandra*" forms, but this difference hardly obtains in the areas where the two forms meet.

The boundaries between the two types of male genitalia are found in Arabia and in Algeria (figs. 7–9). In Arabia the dividing line is identical with that between *Papilio demoleus* and *P. demodocus*, while in Western Algeria the line is oblique, sloping south-west from the Mediterranean coast. As yet, the boundary between the two forms in Algeria has not been correlated with any topographical feature, past or present. Although a considerable number of male specimens have been examined, none has been found in which the genitalia and habitat are not in accord with the above-mentioned boundary lines.

Lampides boeticus (Linnaeus). The British immigrant "Long-tailed Blue" is widely distributed in Southern Europe, throughout Africa, from Arabia to India and Ceylon, and eastwards through the Malay Archipelago to Australia and the Hawaiian Islands. No geographical variation is found in the adult.

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FIG. 7.—The distribution of *Zizeeria knysna* (Trimen). The area with the "*knysna*" type of male genitalia is shaded with vertical lines, and the area with the "*karsandra*" type of genitalia is dark shaded. The forms from the Canary Islands, Cape Verde Island, Mauritius, Comoro Islands, Seychelles and Socotra are of the "*knysna*" type, while those from the Andaman and Nicobar Islands pertain to the "*karsandra*" type.

Pelopidas mathias (Fabricius) is widely distributed in the Aethiopian and Oriental Regions, being found in tropical Africa and Madagascar, and from Ceylon and India to Japan and New Guinea. All the representatives can be divided among four geographical races, and individual variation is more marked than usual in the family.

(*c*) ORIENTAL SPECIES PRESENT IN MADAGASCAR AND TROPICAL AFRICA, BUT ABSENT FROM ARABIA (the *Leptosia alcesta*-complex, *Eurema brigitta* (Cramer), *Melanitis leda* (Linnaeus), *Phalanta phalantha* (Drury), *Libythea narina* Godart, *Zizina otis* (Fabricius) and *Parnara naso* (Fabricius)).

The *Leptosia alcesta*-complex. It seems probable that the genus *Leptosia* Hübner is African in origin and has later reached the Oriental Region, for two

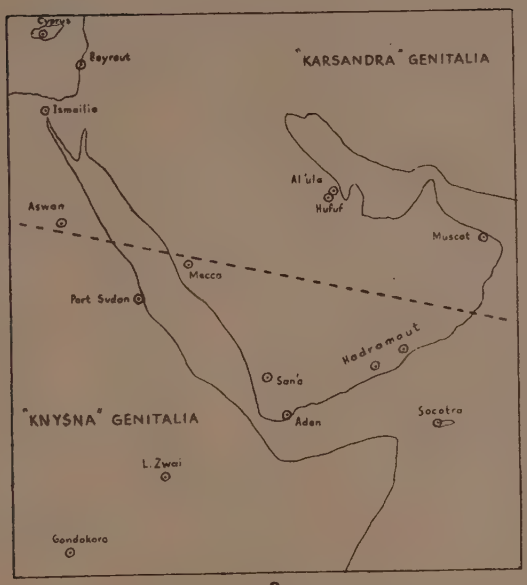

FIG. 8.—*Zizeeria knysna* (Trimen) in Arabia, showing the distribution of the "*karsandra*" and "*knysna*" types of male genitalia.

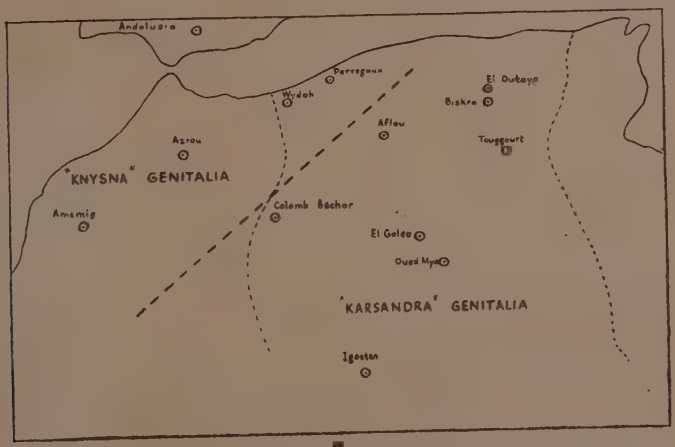

FIG. 9.—*Zizeeria knysna* (Trimen) in Algeria, showing the distribution of the "*karsandra*" and "*knysna*" types of male genitalia.

or three species are found in Africa against one in the East. The difference in the male genitalia between *L. alcesta* (Cramer) (tropical Africa) and *L. nina* (Fabricius) (Ceylon and India to Malaysia and the Celebes) may be only subspecific (fig. 10). The geographical variation is rather less than is indicated by the number of subspecies described.

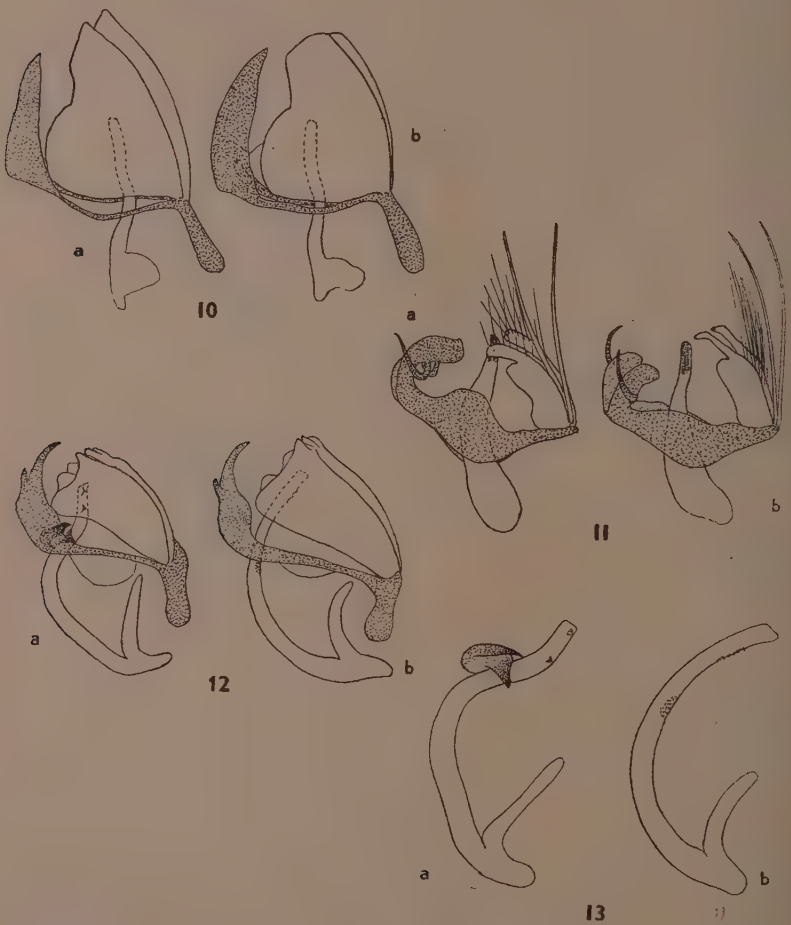

Fig. 10.—Male genitalia (lateral view) of (*a*) *Leptosia alcesta* (Cramer), Madagascar, and (*b*) *L. nina* (Fabricius), Malaya.

Fig. 11.—Male genitalia (lateral view) of (*a*) *Zizina otis* (Fabricius) form "*antanossa*" Madagascar, and (*b*) *Z. otis* (Fabricius) form "*otis*," Java.

Fig. 12.—Male genitalia (lateral view) of (*a*) *Catopsilia pomona* (Fabricius), Madagascar, and (*b*) *C. pomona* (Fabricius), Burma.

Fig. 13.—Aedeagus (lateral view) of (*a*) *Catopsilia pomona* (Fabricius), Madagascar, and (*b*) *C. pomona* (Fabricius), Burma.

The systematics of the genus is in such poor shape that it is not possible to assess the number of species, nor to determine the precise relationship between the African and Oriental forms pending a thorough revision of the genus.

Eurema brigitta (Cramer) is found in tropical Africa and from Ceylon and India to New Guinea, the Bismarck Archipelago and Australia, although the species seems to be missing from several of the Malay Islands where its presence would be expected. As a rule, racial differences are not marked, but the Malagasy subspecies differ much more from the African and Oriental races than the latter do from each other.

Melanitis leda (Linnaeus) is found in tropical Africa, including the Seychelles and some of the Mascarene Islands, and is widely distributed in the Indo-Australian Region from Ceylon and India to Australia, the Fijis, Tahiti and Samoa. Throughout its range the species shows much individual variation, and, in countries with alternating wet and dry seasons, there is a well-developed seasonal dimorphism ; subspecific variation is quite well marked.

Phalanta phalantha (Drury) is distributed from Ceylon and India to Japan, the Philippines and Lesser Sunda Islands, and occurs also in tropical Africa. On Madagascar and on some other islands, there occur other species closely allied to *P. phalantha*. This latter species shows little individual or subspecific variation.

Libythea narina Godart. Usually the Aethiopian forms are regarded as pertaining to a separate species, *L. labdaca* Westwood, but the male genitalia of the two are similar, and the only constant difference found in the adults is that the hind wing is produced at vein 2 in the African representative.

L. narina occurs in tropical Africa as far north as Sudan, and is found from Siam and Malaysia eastwards to the Moluccas.

Zizina otis (Fabricius). Like *Zizeeria knysna* and *Zizula hylax* this butterfly has a low, feeble flight, and it is probable that the adult does not move far. Nevertheless, it flies in tropical and subtropical Africa and in Madagascar, and is common and widely distributed almost throughout the Indo-Australian Region from Ceylon and India to Japan, Australia, New Zealand, and across the Pacific Ocean to Tonga, Samoa and the Society Islands.

As in *Z. knysna* the male genitalia show two distinct types of valva according to locality. The "*otis*" type, with the terminal arm long and narrow, occurs in Assam and eastwards, while the "*antanossa*" type, with the terminal arm shorter and broader, is found in Africa and Madagascar, and in Ceylon and Peninsular India as far east as Bengal (fig. 11).

In both sexes of the African form the upper surface is shining greenish blue, while the colour is bluish purple in the Indo-Australian Region. As a rule, the post-discal spots on the underside of both wings are black in the African forms, only those on the fore wing are black in Ceylon and Peninsular India, and they are not blackened on either wing in the forms from the rest of the Indo-Australian Region. Thus, the difference in facies is related to the difference in male genitalia. In general, individual variation is slight.

Parnara naso (Fabricius). One of the most widely distributed species of HESPERIIDAE, being found in Africa, including Madagascar and the Mascarene Islands, and from Ceylon and India to China, the Moluccas and Australia. The male genitalia show slight differences in the contours of the uncus and the

valva between the African and Oriental forms. As usual in the family, individual variation is slight, but several geographical races can be recognized.

(*d*) Oriental species present in Madagascar but absent from Africa and Arabia (*Catopsilia pomona* (Fabricius) and *Hypolimnas bolina* (Linnaeus)).

Catopsilia pomona (Fabricius). There has been a prolonged controversy as to whether *C. pomona* and *C. crocale* (Cramer) comprise one or two species, but the evidence summarized by Wheeler (1943) leaves little doubt that there is only a single specific entity.

C. pomona is a common secondary growth species, distributed from Ceylon and India to China, Australia and the Solomon Islands, and it is remarkable for its occurrence in two primary forms in each sex. The butterfly occurs also in Madagascar and Mauritius, where it is found in the same two primary forms which, it need hardly be said, were previously regarded as distinct species. In general, the geographical variation is rather slight, and the Madagascan and Mauritius representatives are much more strongly differentiated than are any other subspecies. These African forms are also remarkable in that the aedeagus differs constantly in the number, arrangement and size of the spines from the Oriental forms (figs. 12 and 13).

Hypolimnas bolina (Linnaeus). There is a little evidence suggesting that this butterfly is carried by wind currents, and the approximately constant direction of these currents may account for the division of the species into a large number of quite well-defined geographical races in the more remote parts of its extensive range, in spite of its pronounced migratory tendencies. The species shows considerable variation; indeed, Fruhstorfer regarded it as the most variable butterfly in the world.

In the Aethiopian Region the species is found only in Madagascar, the Seychelles and Mauritius (where it is very rare), but, in the Indo-Australian Region, it is distributed from India and Ceylon, through the Archipelago, and as far east as Tahiti, Samoa and the Marquesas Islands. Specimens from Madagascar in the British Museum appear to be exactly similar to individuals of the Ceylon representative of the species.

Discussion.

Of the twenty-two species of butterflies common to Madagascar and the Oriental Region listed in Table I, it will be noticed that only two are absent from the African mainland. So the majority have no special connection with Madagascar, although in *Anaphaeis aurota* and *Eurema brigitta* the Malagasy race differs from the representatives from the African mainland and Indo-Malaya much more than these differ from each other. In the present discussion it must not be overlooked that some of the species may have had their origins on the western side of the Indian Ocean and spread eastwards from the Aethiopian Region, instead of having moved in the reverse direction. This seems improbable, however, except with *Papilio demoleus*, *Leptosia alcesta*, *Precis orithya*, *Hypolimnas misippus*, *Libythea narina*, and, possibly, *Parnara naso*. In either case the problem resolves itself into a discussion as to how the butterflies crossed the Indian Ocean, and the direction of movement is of secondary importance.

TABLE I.—*Distribution of Species of Rhopalocera Common to Madagascar and the Oriental Region.*

	America.	Madagascar.	Tropical Africa.	Abyssinia.	Arabia.	Ceylon.	Malaysia.
Precis orithya	X	X	X	X	X	X	X
Vanessa cardui	X	X	X	X	X	X	X
Hypolimnas misippus	X	X	X	X	X	X	X
Zizula hylax	X	X	X	X	X	X	X
Papilio demoleus-complex	—	X	X	X	X	X	X
Anaphaeis aurota	—	X	X	X	X	X	—
Catopsilia pyranthe	—	X	X	X	X	X	X
Eurema hecabe	—	X	X	X	X	X	X
Danaus chrysippus	—	X	X	X	X	X	X
Precis lintingensis	—	X	X	X	X	X	—
Lampides boeticus	—	X	X	X	X	X	X
Zizeeria knysna	—	X	X	X	X	X	X
Pelopidas mathias	—	X	X	X	X	X	X
Leptosia alcesta-complex	—	X	X	X	—	X	X
Eurema brigitta	—	X	X	X	—	X	X
Melanitis leda	—	X	X	X	—	X	X
Phalanta phalantha	—	X	X	X	—	X	X
Libythea narina	—	X	X	S. Sudan	—	—	X
Zizina otis	—	X	X	X	—	X	X
Parnara naso	—	X	X	S. Sudan	—	X	X
Catopsilia pomona	—	X	—	—	—	X	X
Hypolimnas bolina	—	X	—	—	—	X	X

Assuming that all direct land connection between Madagascar and the Indo-Malayan lands disappeared long before the present species of Rhopalocera came into existence (see Zeuner, 1946 : 377), there appear to be three ways in which the species under discussion may have reached Madagascar from the Oriental Region (or *vice versa*, with a few species) : (*a*) overland movement, (*b*) overseas movement, (*c*) human agency.

(a) *Overland movement.*

In any overland movement in comparatively recent times, the butterflies must have travelled between Indo-Malaya and Madagascar *via* India and Arabia. Even so, there still remains the sea journey of about 100 miles across the Mozambique Channel.

Such a movement might explain the presence of a few species (perhaps *Catopsilia pyranthe*, *Eurema hecabe*, *Danaus chrysippus*, *Precis lintingensis*, *Lampides boeticus* and *Pelopidas mathias*), where there are no sharp changes in form or structure between the Malagasy and the Oriental forms, and, indeed, where there is almost a cline present from Indo-Malaya through Arabia and Africa to Madagascar. It cannot explain the presence of *Papilio demoleus* and *Zizeeria knysna*, with a sharp boundary between the two genitalia forms in Arabia, nor of *Anaphaeis aurota*, in which the Madagascar race is very distinct from the nominotypical form which flies from East Africa to India and Ceylon.

(*b*) *Overseas movement.*

The butterfly species most likely to be distributed over a wide area as a consequence of chance dispersal are those in possession of a well-developed migratory tendency. It has been pointed out already that, in the equatorial regions the migratory butterflies are, almost invariably, secondary growth species in which the presence of a migratory instinct probably saves them from, at least, local extinction. It was shown (Corbet, 1941) that the continued existence of certain tropical species of Rhopalocera, whose larvae feed on plants confined to a particular stage in the reversion from cleared land to primary forest, depends on the adults moving on to another area when the food plants disappear in the course of the regeneration process.

Of the four criteria suggested by Wiltshire (1946 : 172) for recognizing migratory species of butterflies, the first three have been assessed for the species under discussion in Table II, according to information given in Williams (1930) and in Williams, Cockbill, Gibbs and Downes (1942). The provisions which should be fulfilled, according to Wiltshire, are :

(i) The species has been observed performing a mass movement.
(ii) It has been taken or seen on the wing at sea.
(iii) It shows no geographical variation over a wide and diverse area.
(iv) Both sexes occur occasionally, or sporadically, far from where it is known to breed or reside.

The last criterion has been omitted from consideration here as, in most cases, the available information is insufficient to decide whether or not this condition is fulfilled.

In columns (i) and (ii) in Table II each X represents a single satisfactory record, while XXX indicates three or more records. The geographical variation in column (iii) is roughly proportional to the number of crosses.

If the presence on both sides of the Indian Ocean of the butterflies under consideration is due, in a large measure, to the possession of migratory tendencies, it would be anticipated that almost all the species would be present on the continental islands, and they would be strongly represented on the oceanic islands in the Indian Ocean (fig. 7). As Table III shows, this is, indeed, largely the case, although there are several surprising lacunae. The circumtropical species *Precis orithya* and *Hypolimnas misippus* are absent from, or very rare in, the Andaman and Nicobar Islands, *Phalanta phalantha* is not found on the former islands, and *Precis lintingensis* is absent from the latter. It will be noticed that the common citrus-feeding *Papilio demoleus* is also absent from these islands, as it is from the Large Sunda Islands, the Philippines, Celebes and Moluccas. The absence of *Pelopidas mathias* and *Parnara naso* from the Andaman and Nicobar Islands is less surprising, as the larvae feed on rice.

Again, if the presence of these species on both sides of the Indian Ocean is attributable mainly to migratory tendencies, it would be expected that, as a first approximation, the number of these species present on an oceanic island in this Ocean would be proportional to the area of the island in question and inversely proportional to its distance from the nearest mainland. As ecological and geological factors also intervene, it is difficult to test this relationship

TABLE II.—*Migratory Details of the Species of Rhopalocera Common to Madagascar and the Oriental Region.*

	If recorded as migratory by Williams (M).	(i) Mass movements observed.	(ii) Seen at sea.	(iii) Geographical variation.
Precis orithya	M	XXX	X	XX
Vanessa cardui	M	XXX	XXX	—
Hypolimnas misippus	M	XXX	XXX	—
Zizula hylax	—	—	—	—
Papilio demoleus-complex	M	XXX	X	X
Anaphaeis aurota	M	XXX	—	X
Catopsilia pyranthe	M	XXX	X	X
Eurema hecabe	M	XX	X	XX
Danaus chrysippus	M	XX	—	X
Precis lintingensis	M	X	—	X
Lampides boeticus	M	XXX	—	—
Zizeeria knysna	—	—	—	X
Pelopidas mathias	M	X	—	—
Leptosia alcesta-complex	—	—	—	XX
Eurema brigitta	—	—	—	X
Melanitis leda	—	—	—	XX
Phalanta phalantha	M	XXX	—	X
Libythea narina	M	XXX	—	X
Zizina otis	—	—	—	XX
Parnara naso	—	—	—	—
Catopsilia pomona	M	XXX	—	X
Hypolimnas bolina	M	X	—	XX

adequately, but it will be noticed that the more remote the island, the higher the proportion of the species in Table I to the total Rhopalocera species present.

It is possible that *Hypolimnas bolina* is distributed by wind currents, and the identity of the Malagasy representative with that from Ceylon may be significant in this connection. It is difficult to prove such a thesis, however, and the currents in the upper strata of the air may be in a different direction from those nearer the ground. *H. bolina* occurs in a number of distinct geographical races between Ceylon and the Marquesas Islands, in the eastern Pacific Ocean, and it may well be that these races are an indication of the wind currents prevailing in the upper atmosphere in the Pacific Ocean.

It is evident that the migration theory can be evoked to explain the presence of only a proportion of the butterfly species found on both sides of the Indian Ocean. There is clearly no evidence of continuous or recent colonization across the Ocean by such species as *Papilio demoleus*, *Leptosia alcesta*, *Anaphaeis aurota*, *Catopsilia pomona*, *Eurema brigitta*, *Libythea narina*, *Zizeeria knysna*, *Zizina otis*, *Parnara naso* and *Pelopidas mathias*.

It may be mentioned in passing, that, in reviewing the flora of Madagascar, Baron (1889) found that very few of the plants peculiar to the island had oriental affinities, and that these few species appeared to be confined mainly to the east coast.

TABLE III.—*Distribution of Species of Rhopalocera Common to Madagascar and the Oriental Region on Islands in the Indian Ocean.*

	Mauritius (*Vinson*, 1938).	Seychelles (*Fryer*, 1912).	Socotra (*Ogilvie-Grant*, 1903).	Maldive and Laccadive Islands (*Meyrick*, 1902).	Chagos Archipelago (*Fletcher*, 1910).	Andaman Islands (*Evans*, 1932).	Nicobar Islands (*Evans*, 1932).	Christmas Island (*Butler*, 1900, *Pendlebury*, 1933).	Cocos-Keeling Islands (*C. A. Gibson-Hill*, in *litt.*, 18.xii.1947).
Precis orithya	—	X	—	—	—	—	(X)	—	—
Vanessa cardui	X	X	X	X	—	X	X	X	X
Hypolimnas misippus	X	X	X	—	—	(X)	(X)	X	X
Zizula hylax	X	X	—	X	—	X	X	X	—
Papilio demoleus-complex	X	—	X	—	—	—	—	—	—
Anaphaeis aurota	—	—	—	—	—	—	(X)	—	—
Catopsilia pyranthe	X	X	X	—	—	X	—	—	—
Eurema hecabe	X	—	—	—	—	X	X	X	—
Danaus chrysippus	X	X	X	—	—	X	X	X	X
Precis lintingensis	—	—	—	—	—	X	—	—	—
Lampides boeticus	X	X	—	—	—	X	X	—	—
Zizeeria knysna	X	X	X	—	—	X	X	—	—
Pelopidas mathias	—	—	—	—	—	—	—	—	—
Leptosia alcesta-complex	—	—	—	—	—	X	X	—	—
Eurema brigitta	X	X	—	—	—	—	—	—	—
Melanitis leda	X	X	—	—	—	X	X	X	—
Phalanta phalantha	X	X	X	—	—	—	X	—	—
Libythea narina	—	—	—	—	—	—	—	—	—
Zizina otis	X	—	—	—	—	X	X	—	—
Parnara naso	X	—	—	—	—	—	—	—	—
Catopsilia pomona	X	—	—	—	—	X	(X)	X	—
Hypolimnas bolina	X	X	—	—	X	X	X	X	X
Total Rhopalocera species recorded	38	27	28	10	2	170	99	15	5

(X) indicates that the species has been recorded from the Andaman or Nicobar Islands, but that there are no specimens in the British Museum.

(c) *Accidental transportation by human agency.*

Curiously enough a certain amount of evidence can be adduced in support of the view that human agency has been responsible for the movement across the Indian Ocean of some of the species listed in Table I.

With the exception of the truly migratory *Hypolimnas bolina*, all these species feed on one or more plants that are cultivated in India for various domestic purposes (food, medicine, dyeing, making fibre, etc.) (see Watt, 1889-1893). On the other hand, it must not be overlooked that many, if not most, secondary growth butterflies now have one or more larval food plants among cultivated forms.

In the early centuries of the Christian Era, there was much activity in the seas around South-east Asia, and emigrants from South India sailed to such distant lands as Indo-China, the Large Sunda Islands and Celebes, where

often they settled and merged with the native population. Although these Indian argonauts themselves kept no records, their exploits are referred to in the writings of contemporary Chinese travellers. For example, it has been established that Indianized emigrants from Sumatra colonized Madagascar quite early in the Christian era (*ca.* VIIth and VIIIth centuries), and, indeed, traces of their language and customs are said to survive in the island to-day, although it is possible that this Malayan influence is not as strong as many writers suppose, for there are almost no Malagasy place names or words indicative of Malay origin.

These early voyages took place in massive ships, carrying over a hundred souls, and in which plants were cultivated for food, and, doubtless, for other domestic purposes. If this cultivation was on the large scale it appears to have been, it may be supposed that lepidopterous species whose larvae fed on the plants would also be transported occasionally in various stages of development. It is probable that these voyages between Madagascar and the Malay lands were discontinued not later than the XVth century, and it seems there has been no regular intercourse in recent centuries.

If any of our butterflies were first transported across the Indian Ocean by these early travellers, it must be assumed that they reached the African mainland in due course and became widely distributed throughout the equatorial belt. Moreover, with some species, such as *Papilio demoleus* and *Zizeeria knysna*, it must be supposed also that they remained isolated in Madagascar long enough to develop distinctive genitalia characters before crossing to the African mainland. In the case of *Catopsilia pomona* it would appear that, while the species has remained isolated in Madagascar long enough for the male to develop distinct genitalia characters, it has not yet crossed the Mozambique Channel to the African mainland, although the Malagasy form occurs also in Mauritius.

If transportation by human agency in the manner described were indeed the explanation of the presence of these species on both sides of the Indian Ocean, in some cases an approximate estimate could be made of the length of time required for certain fundamental changes in structure. The time limits would lie between 1000 and 1500 years, which most palaeontologists would consider much too short a time. For example, the British race of the " Large Copper " butterfly *Lycaena dispar* (Haworth), is only separable from the Dutch subspecies on coloration and in a series, and yet the colonies of these two forms have been separated for about 7500 years. The Jersey race of the Tettigoniid grasshopper *Platycleis occidentalis* Zeuner can be distinguished from the form from Western Europe and Southern England on structural differences, but Jersey has been isolated from France for 7000 to 10,000 years (Zeuner, 1946, chapter xii). According to this same author, the maximum rate of species formation is 500,000 years per species-step, so that human agency must be entirely ruled out as being responsible for the presence of such species as *Papilio demoleus*, *Leptosia alcesta*, *Catopsilia pomona*, *Libythea narina*, *Zizeeria knysna* and *Parnara naso* on both sides of the Indian Ocean.

We are, indeed, driven to the conclusion that chance dispersal across the seas in the remote past is the most likely explanation for the presence of the species listed on both sides of the Indian Ocean. The presence of more than a single species of the *Phalanta phalantha*-complex on several islands suggests

several successful colonizations by this butterfly at intervals of at least half a million years.

It seems probable that the presence of the genera and genera-groups common to Madagascar and the Oriental Region must be explained along the same lines, although, of course, much greater periods of time are involved, and, in the case of *Henotesia*, considerable local species formation must have occurred in Madagascar at a time when the prototype of the present species was in a more plastic stage from the evolutionary standpoint.

Summary.

A survey of the Rhopalocera of Madagascar has shown there are four or five genera with strong Oriental affinities which are absent from, or only sparsely represented on, the African mainland. The single species of *Atrophaneura* is certainly an aberrant member of the genus, while the Malagasy species of *Henotesia* are intermediate between the Oriental *Mycalesis* and the African *Monotrichtis*.

Most of the twenty-two species common to Madagascar and the Oriental Region have pronounced migratory tendencies, and it seems probable that they crossed the Indian Ocean by the aid of wind and wave currents at various times in the remote past. In *Papilio demoleus*, *Leptosia alcesta*, *Catopsilia pomona*, *Libythea narina*, *Zizeeria knysna* and *Parnara naso*, structural differences are present in representatives from the two sides of the Indian Ocean, indicating long separation and no recent colonization. In *Anaphaeis aurota* and *Eurema brigitta* the Malagasy race differs more widely from the African and Oriental representatives than these do from each other.

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